Plant Cell Physiol. 32(3): 433–438 (1991)

Effects of 2-Deoxygalactose on Auxin-Induced Growth and Levels of UDP-Sugars in Higher Plants

Masahiro Inouhe[1] and Ryoichi Yamamoto[2]

[1] *Department of Biology, Faculty of Science, Ehime University, Matsuyama, 790 Japan*
[2] *Laboratory of Biology, Tezukayama College, Nara, 631 Japan*

Galactose inhibited the IAA-induced elongation of cells in segments of oat coleoptiles but not in segments of azuki bean and cucumber stems. In contrast, its analogs, 2-deoxygalactose and 2-deoxyglucose, inhibited the IAA-induced elongation of cells in these plant tissues. In segments of cucumber stems, 2-deoxygalactose inhibited formation of cell-wall polysaccharides with little effect on respiration in terms of either reduced consumption of O_2 or levels of ATP. 2-Deoxygalactose and 2-deoxyglucose caused a rapid decrease in the levels of UTP and UDP-sugars with a concomitant increase in levels of UDP in cucumber segments. These results suggest that 2-deoxysugars inhibit synthesis of cell-wall polysaccharides by decreasing the levels of UDP-sugars, thereby inhibiting IAA-induced elongation of cells in cucumber segments. 2-Deoxysugars can, therefore, be used as potential inhibitors with which to assess the role of UDP-sugars in the IAA-induced elongation of cells in dicotyledonous plants.

Key words: Cell elongation — Cell-wall synthesis — 2-Deoxy-D-galactose — D-Galactose — Stem and coleoptile — UDP-glucose.

Galactose has been reported to inhibit growth of many tissues of monocotyledonous plants. This sugar inhibits the IAA-induced elongation of cells in segments of cereal coleoptiles (Baker and Ray 1965, Ordin and Bonner 1957, Yamamoto et al. 1981), the growth of maize root tips (Göring and Reckin 1968, Tanimoto et al. 1989), the proliferation of *Lemna* fronds (DeKoch et al. 1979) and division of cells of wild sugarcane in suspension culture (Maretzki and Thom 1978). Galactose has been demonstrated to inhibit specifically the synthesis of cell-wall polysaccharides in segments of oat coleoptiles (Yamamoto and Masuda 1984). This sugar, after its conversion to galactose-1-phosphate, inhibits the formation of UDP-glucose in the following two ways: via consumption of endogenous UTP for the preferential accumulation of UDP-galactose and via a competitive inhibition of the enzymatic reaction (Inouhe et al. 1986, 1987, Yamamoto et al. 1988). These results suggest the importance of the metabolism of UDP-sugars in growth of monocotyledonous plants.

Galactose has little effect on the growth of dicotyledonous plants, in general. Galactose does not inhibit the IAA-induced elongation of cells in stem segments from several dicotyledonous plants, in which it has little effect on the formation of UDP-glucose (Inouhe et al. 1987b, Yamamoto et al. 1988). In addition, galactose is known to function as a substrate for growth in many dicotyledonous tissues (Göring and Reckin 1968, Gross et al. 1981). Galactose, thus, cannot be used as a probe for investigating the role of the UDP-glucose pathway in dicotyledonous plants.

2-Deoxyglucose has been extensively used as an analog for determining the rates of uptake and transport of hexoses, especially in animal cells (Jacobs et al. 1990). 2-Deoxyglucose is also known to inhibit the glycosylation of glycoproteins in animal cells (Schwarz and Schmidt 1976) and the synthesis of cell-wall polysaccharides in many types of plant (Kratky et al. 1975, Datema et al. 1983, Jaffe and Leopold 1984).

In the present study, we examined the effects of 2-deoxygalactose and 2-deoxyglucose on the IAA-induced elongation of cells and the levels of UDP-sugars in mono- and dicotyledonous plants. We found that the deoxysugars inhibit IAA-induced elongation of cells, probably via a decrease in the levels of UDP-sugars, in dicot-

Abbreviations: GLC, gas-liquid chromatography; HPLC, high-performance liquid chromatography; IAA, indole-3-acetic acid; TFA, trifluoroacetic acid.

yledonous plants.

Materials and Methods

Plant materials—Oat (*Avena sativa* L. cv. Victory) seedlings were grown in the dark for 4 days at 25°C (Sakurai et al. 1977). Azuki bean (*Vigna angularis* Owhi et Ohashi) and cucumber (*Cucumis sativum* L.) seedlings were grown in the dark for 5 days at 25°C (Yamamoto et al. 1988). Coleoptile segments (20 mm long) with first leaves removed or segments of stems were excised from the region 3–23 mm below the tip and pooled in distilled water. The larger segments were cut into 10-mm segments with a double-bladed cutter and incubated with 10 mM MES (pH 6.5) with or without 10 μM IAA and 10 mM sugar (galactose, 2-deoxygalactose or 2-deoxyglucose). After appropriate periods of incubation, the lengths of sections were measured with a binocular microscope (×6.3) equipped with an ocular micrometer, under a dim green light at 25°C.

Isolation of UDP-sugars and nucleotides—The extraction and purification of UDP-sugars were performed as reported previously (Standard et al. 1983, Inouhe et al. 1987b) with slight modifications. One hundred sections from individual stems, which had been frozen and stored at −80°C in the dark, were homogenized with 2 ml of 0.2 M TFA at 0°C. Each homogenate was centrifuged at 1,500× *g* for 10 min at 0°C and the supernatant was collected and lyophilized to remove water and TFA. The lyophilized material was dissolved in 0.8 ml of distilled water and a 0.5-ml portion of the solution was loaded onto a Partisil SAX column (Whatman Ltd., Kent, ME). The column was eluted with a non-linear gradient of sodium dihydrogenphosphate. The amounts of the various nucleotides separated were determined from the absorbance of each at 260 nm and recovery of corresponding authentic nucleotides, as described previously (Inouhe et al. 1987b).

Determination of sugar moieties of UDP-sugars—The fraction of UDP-sugars, obtained by HPLC, was collected and lyophilized. Each lyophilized sample was hydrolyzed in 2 M TFA at 121°C for 90 min to allow the efficient hydrolysis of salt-contaminated materials. The released sugar moieties were dried, reduced, and acetylated (Albersheim et al. 1967, Sakurai et al. 1979). The amounts of acetylated sugars were determined with a gas-liquid chromatograph (Hitachi model 663) equipped with a capillary column (SP-2330, Supelco Inc., Bellefonte, PA).

Determination of cell-wall polysaccharides—Segments of coleoptiles and stems were killed by immersion in boiling methanol for 5 min. They were then treated with pancreatic α-amylase (Sigma Chemical Co., St Louis, MO) and with Pronase E (Kaken Kagaku Co., Ltd., Tokyo) for 12 h at 37°C in each case. The Pronase-treated materials were washed three times each with distilled water, acetone, and a mixture of chloroform and methanol (1 : 1, v/v) and air-dried at 37°C. The dried cell-wall preparation was hydrolyzed with 2 M TFA for 90 min at 121°C to liberate the neutral sugar components of non-cellulosic polysaccharides (Albersheim et al. 1967, Sakurai et al. 1979). The neutral sugar components were identified by GLC as described above. The cell-wall residue, which had not been hydrolyzed by 2 M TFA, was regarded as cellulose. The sugar content in this fraction was determined by the phenol sulfuric acid method after hydrolysis with 72% (v/v) sulfuric acid (Inouhe et al. 1987a).

Determination of tissue respiration—Rates of respiration of cucumber stem tissues were estimated in term of absorption of oxygen in the dark at 25°C, by the method of Fujii et al. (1985). Twenty segments of stems treated with IAA and/or sugars for 2 h were dipped in 2.7 ml of distilled water and absorption of oxygen was measured with an oxygen electrode (Bioxygraph; Kyusui Kagaku, Tokyo).

Results

Effects of galactose and 2-deoxygalactose on IAA-induced elongation of cells in mono- and dicotyledonous plants—Figure 1 shows the effects of 2-deoxygalactose on the IAA-induced elongation of cells in oat coleoptile segments. 2-Deoxygalactose (10 mM) inhibited the IAA-induced elongation of cells after a lag of 1–2 h and normal elongation was restored when it was removed from the incubation medium, as in the case of galactose (Yamamoto et al. 1981, Inouhe et al. 1986). This result suggests that 2-de-

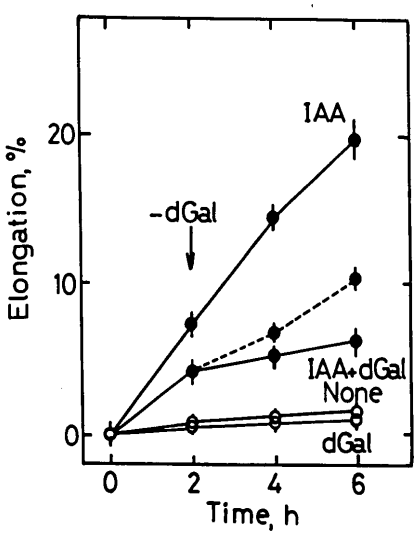

Fig. 1 Effect of 2-deoxygalactose on IAA-induced elongation of cells in segments of oat coleoptiles. Coleoptile segments (10 mm long) were incubated in 10 mM MES (pH 6.5) that contained 10 μM IAA and/or 10 mM 2-deoxygalactose. Broken line, 2-deoxygalactose removed at 2 h (arrows). Vertical bars denote standard errors (n=20).

oxygalactose may have a similar effect to that of galactose on IAA-induced growth in monocotyledonous plants.

Galactose (10 mM) had no marked effect on IAA-induced elongation of cells in segments of stems of azuki bean and cucumber (Figs. 2A and B), as reported previously (Yamamoto et al. 1988). 2-Deoxygalactose, by contrast, strongly inhibited IAA-induced elongation of cells in these segments (Figs. 2C and D). 2-Deoxyglucose also inhibited IAA-induced elongation of cells in cucumber segments (Fig. 2D), as did 2-deoxygalactose.

Effects of 2-deoxygalactose on the levels of cell-wall polysaccharides in segments of cucumber stems—Table 1 shows the effects of 2-deoxygalactose on the levels of neutral sugar components in the non-cellulosic fraction of segments of cucumber stems. The major components in this fraction were arabinose, xylose, galactose and glucose. In the absence of 2-deoxygalactose, levels of these sugars increased after a 6-h incubation both in the presence and the absence of IAA. IAA stimulated the increases in the levels of sugar, by 10–20% in the case of arabinose, galactose and glucose, and by 65% in the case of xylose. 2-Deoxygalactose strongly inhibited the increases in the levels of the non-cellulosic components in both the presence and the absence of IAA. 2-Deoxygalactose also inhibited the increase in levels of cellulosic polysaccharides during a 6-h incubation (data not shown). These results suggest that 2-deoxygalactose inhibits the overall synthesis of cell-wall polysaccharides in segments of cucumber stems.

Effects of 2-deoxysugars on the levels of UDP-sugars and uridine nucleotides in segments of cucumber stems—Figure 3 shows the effects of 2-deoxygalactose and of 2-deoxyglucose on the levels of UTP, UDP and UDP-sugars in segments of cucumber stems after 2 h. Both in the presence and absence of IAA, 2-deoxysugars caused a 60–70% decrease in the levels of UDP-sugars, key intermediates in the synthesis of cell-wall polysaccharides (Ordin and Hall 1968, Hassid 1969, Carpita and Delmer 1981). 2-Deoxysugars also caused a large increase in levels of UDP and a decrease in levels of UTP in the segments irrespective of the presence or absence of IAA. Both the 2-deoxysugars and IAA had no marked effect on the apparent total levels of uridine nucleotides (UDP-sugars + UTP + UDP).

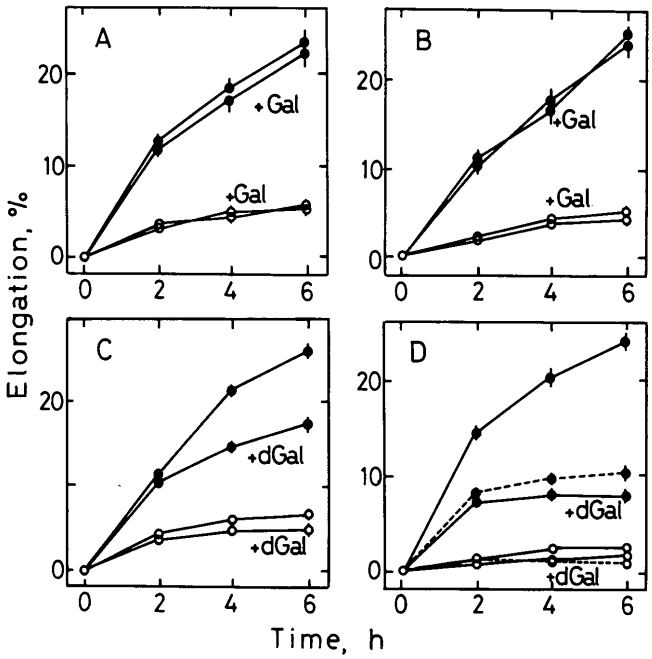

Fig. 2 Effects of galactose and 2-deoxygalactose on IAA-induced elongation of cells in stem segments. Stem segments (10 mm long) were incubated with 10 mM MES (pH 6.5) that contained 10 μM IAA and/or 10 mM galactose (A, B) or same buffer containing 10 μM IAA and/or 10 mM 2-deoxygalactose (C, D). A and C, segments of azuki bean stems; B and D, segments of cucumber stems. Broken lines, treatment with 10 mM 2-deoxyglucose. Open symbols, minus IAA; solid symbols, plus IAA. Vertical bars denote standard errors (n=20).

Table 1 Effects of 2-deoxygalactose (dGal) on the levels of sugars in non-cellulosic fractions of cell walls from cucumber stems

Treatment	Rhamnose	Arabinose	Xylose	Mannose	Galactose	Glucose
			μg/segment (%)			
Initial	37.1 (100)	42.2 (100)	64.4 (100)	27.3 (100)	181.5 (100)	82.1 (100)
None	41.1 (111)	47.7 (113)	88.2 (137)	35.8 (131)	194.7 (108)	96.7 (118)
IAA	40.3 (109)	57.0 (134)	145.7 (220)	35.0 (128)	233.1 (129)	106.0 (129)
dGal	37.1 (100)	42.4 (100)	83.4 (126)	31.8 (116)	181.5 (101)	87.4 (107)
IAA + dGal	35.8 (96)	39.7 (94)	79.5 (120)	29.7 (109)	177.5 (99)	82.1 (100)

Twenty segments of stems were incubated in 10 mM MES (pH 6.5) that contained 10 μM IAA and/or 10 mM 2-deoxygalactose for 6 h. The cell walls were prepared and hydrolyzed with 2 M TFA, and the liberated neutral sugars were subjected to analysis by GLC.

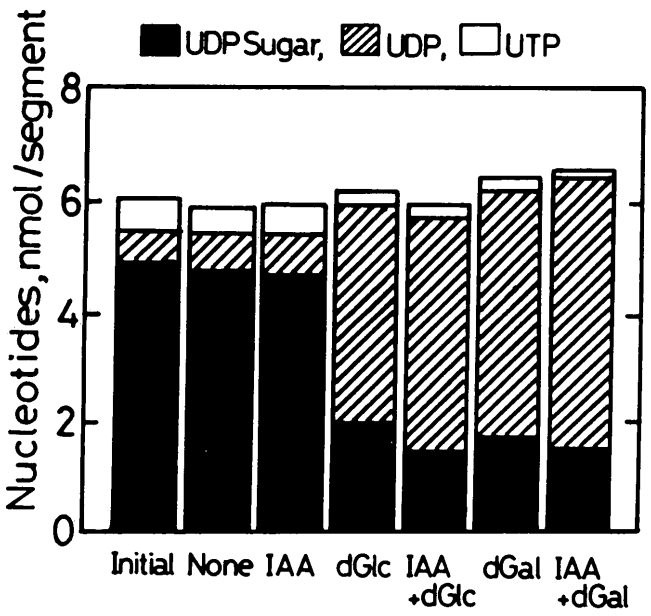

Fig. 3 Effects of 2-deoxygalactose and 2-deoxyglucose on the levels of uridine nucleotides in segments of cucumber stems. Stem segments (10 mm long) were incubated with 10 mM MES (pH 6.5) that contained 10 μM IAA, 10 mM 2-deoxygalactose and/or 10 mM 2-deoxyglucose for 2 h. The segments were treated with TFA and the levels of extracted uridine nucleotides were determined by their absorbance at 260 nm after HPLC.

The sugar moieties of the UDP-sugar fraction after treatment with 2-deoxygalactose of segments of cucumber and azuki bean stems were analyzed by GLC (Fig. 4). The major sugar components of the UDP-sugar fractions in cucumber and azuki bean segments were glucose, galactose and xylose. 2-Deoxygalactose caused a reduction of about 50–80% in levels of UDP-glucose in both the presence and absence of IAA in segments of cucumber and azuki bean stems. 2-Deoxygalactose also caused a large decrease in levels of UDP-galactose, especially in azuki bean segments, but it had little effect on the level of UDP-xylose in cucumber and azuki bean segments. 2-Deoxyglucose also caused a decrease in the levels of UDP-hexoses, as did 2-deoxygalactose (data not shown). These results suggest a preferential effect of 2-deoxysugars on UDP-hexoses rather than on UDP-pentoses in stem segments.

Effects of 2-deoxysugars on respiration by cucumber segments—It is possible that 2-deoxysugars have some effect on tissue respiration because of their structural similarity to glucose. Therefore, we examined the effect of 2-deoxysugars on the consumption of oxygen by cucumber stem tissues. The data indicated that neither 2-deoxygalactose nor 2-deoxyglucose inhibited the consumption of oxygen by cucumber segments (control, 0.040–0.042 μmol O_2 h^{-1} $segment^{-1}$; IAA-treatment, 0.040–0.044 μmol O_2 h^{-1} $segment^{-1}$). Furthermore, 2-deoxysugars did not affect levels of endogenous ATP (control, 1.1–1.4 nmol $segment^{-1}$; IAA-treatment, 1.1–1.6 nmol $segment^{-1}$) in cucumber segments in 2 h. These results suggest that 2-deoxysugars have little effect on tissue respiration and, thus, on energy production, at least for 2 h.

Discussion

In segments of oat coleoptiles, 2-deoxygalactose inhibited the IAA-induced elongation of cells (Fig. 1) as did

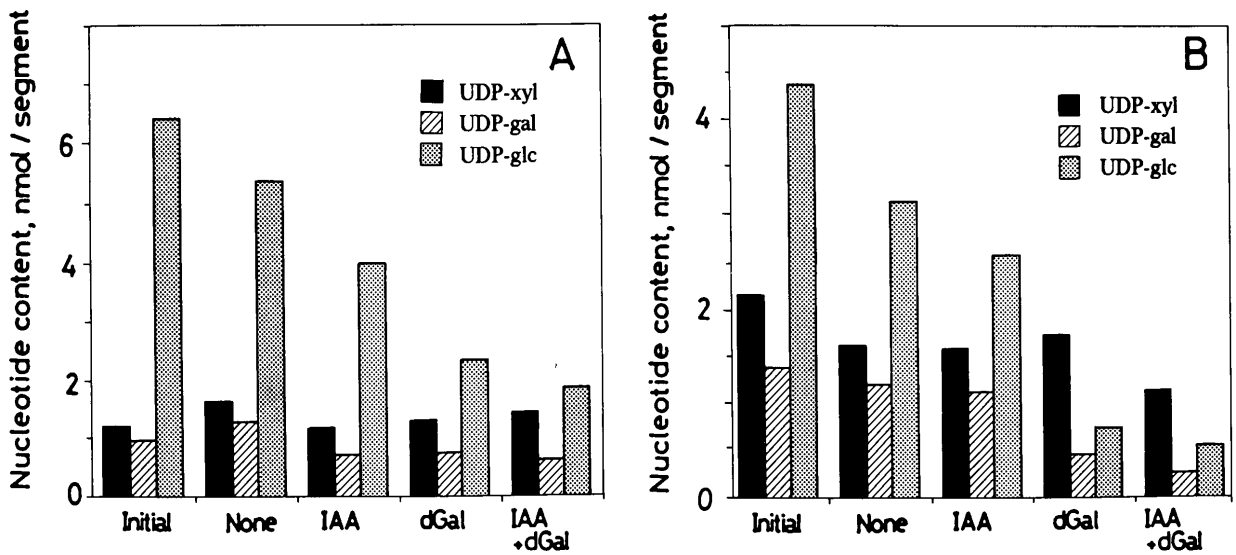

Fig. 4 Effects of 2-deoxygalactose on the levels of UDP-sugars in segments of cucumber and azuki bean stems. Segments of cucumber (A) or azuki bean (B) stems were incubated with 10 mM MES (pH 6.5) that contained 10 μM IAA and/or 10 mM 2-deoxygalactose for 2 h. The sugar moieties in the UDP-sugar fractions separated by HPLC were analyzed by GLC.

galactose (Yamamoto et al. 1981, Inouhe et al. 1987a). This result suggests that these sugars may inhibit a common metabolic event required for the IAA-induced elongation of cells. In previous papers, we reported that galactose specifically inhibits synthesis of cell-wall polysaccharides with little further effect on various other metabolic and physiological processes in segments of oat coleoptiles (Yamamoto and Masuda 1984). 2-Deoxygalactose would, thus, be expected to have an effect on cell-wall synthesis in monocotyledonous plants, just as galactose does.

In dicotyledonous plants, 2-deoxysugars were also capable of inhibiting IAA-induced growth (Fig. 2). This result stands in sharp contrast to the case of galactose, which had little effect on the growth of dicotyledonous plants (Inouhe et al. 1987b, Yamamoto et al. 1988). Galactose is easily metabolized to substrates for growth and synthesis of important metabolites (Gross et al. 1981, Verma and Dougal 1979), and it does not inhibit cell-wall synthesis in many dicotyledonous tissues (Yamamoto et al. 1988). 2-Deoxysugars would be expected to be lacking in these properties, with resultant inhibition of IAA-induced elongation of cells in stem segments. In fact, we found that 2-deoxygalactose strongly inhibited the synthesis of cell-wall polysaccharides in segments of cucumber stems (Table 1), with little effect on the respiration of the tissues.

So far, little has been reported with respect to the effect of 2-deoxygalactose on the synthesis of cell-wall polysaccharides and the related metabolism of sugars in plants. In the present study, we found that this sugar caused a substantial decrease in levels of UDP-sugars, key intermediates in the synthesis of cell-wall polysaccharides. This result suggests that 2-deoxygalactose inhibits the metabolism of UDP-sugars, thereby, inhibiting synthesis of cell wall polysaccharides. Another analog, 2-deoxyglucose, has been reported to inhibit glycosylation of glycoproteins in animal cells (Schwarz and Schmidt 1980), and the synthesis of cell-wall polysaccharides in yeast (Kratky et al. 1975), an alga (Datema et al. 1983) and in pea and maize plants (Jaffe and Leopold 1984). We found that the effects of 2-deoxyglucose on growth, levels of UDP-sugars and tissue respiration were similar to those of 2-deoxygalactose. These results suggest that their modes of actions in relation to cell-extension growth are basically homologous and, possibly, dependent on the metabolism of UDP-sugars.

2-Deoxyglucose has been reported to be taken up by cells via a simple and facilitated diffusion system, being subsequently phosphorylated by hexokinase in human muscle cells (Jacobs et al. 1990). In yeast, 2-deoxyglucose and 2-deoxygalactose are taken up by at least two different active transport mechanisms: the former is taken up by transport-associated phosphorylation and the latter as free sugar by chemiosmotic coupling, with subsequent intracellular phosphorylation (Jaspers and Van Steveninck 1977). It is also known that 2-deoxysugars are readily metabolized to 2-deoxysugar-1-phosphates and UDP-2-deoxysugars in animal and yeast cells (Schwart and Schmidt 1976, Jaspers and Van Steveninck 1976), in reactions that are homologous to the metabolism of galactose in oat coleoptiles (Inouhe et al. 1986). The details of the membrane transport and subsequent metabolism of 2-deoxysugars in plant stem cells are not well known but can potentially be explained by the above mentioned similar mechanisms.

In segments of cucumber stems, 2-deoxysugars caused a decrease in levels of UTP and an increase in levels of UDP (Fig. 3). In this regard, it is interesting to note that the 2-deoxysugars did not affect the apparent levels of total uridine nucleotides (UDP-sugars + UTP + UDP). This observation suggests that they have little effect on the synthesis of uridine nucleotides de novo, suggesting in turn that they may affect the interconversion or recycling of preexisting uridine nucleotides in some manner. The effect might not include any reduction in the source of energy used for the recycling, since 2-deoxysugars had little effect on levels of ATP at least over the course of 2 h. It is to be expected that 2-deoxysugars have some effect on various enzymatic reactions, perhaps those involved in the formation of UTP from UDP or the hydrolysis of UDP-sugars. A preferential decrease in levels of UDP-hexose and a concomitant increase in levels of UDP appear to support the latter possibility, although further mechanistic studies are needed to confirm this hypothesis.

The present experiments on the effects of deoxysugars in mono- and dicotyledonous plants, together with the data on the effects of galactose in monocotyledonous plants, indicate that the cell-wall synthetic pathway, via UDP-glucose, plays an important role in auxin-induced elongation of cells in mono- and dicotyledonous plants.

References

Albersheim, P., Nevins, D. J., English, P. D. and Karr, A. (1967) A method for the analysis of sugars in plant cell wall polysaccharides by gas-liquid chromatography. *Carbohydr. Res.* 5: 340–345.

Baker, D. B. and Ray, P. M. (1965a) Direct and indirect effects of auxin on cell wall synthesis in oat coleoptile tissue. *Plant Physiol.* 40: 345–352.

Baker, D. B. and Ray, P. M. (1965b) Relationships between effects of auxin on cell wall synthesis and cell elongation. *Plant Physiol.* 40: 360–368.

Carpita, N. C. and Delmer, D. P. (1981) Concentration and metabolic turnover of UDP-glucose in developing cotton fibers. *J. Biol. Chem.* 256: 308–315.

Datema, R., Schwarz, R. T., Rivas, L. A. and Lezica, R. P. (1983) Inhibition of β-1,4-glucan biosynthesis by deoxyglucose. The effect on the glucosylation of lipid intermediates.

Plant Physiol. 71: 76–81.

DeKoch, P. C., Cheshire, M. V., Mundie, C. M. and Inkson, R. H. E. (1979) The effect of galactose on the growth of *Lemna*. *New Phytol.* 82: 679–685.

Fujii, S., Yamamoto, R. and Takada, H. (1985) Glycerol formation in *Dunaliella* cells under non-growing conditions with hypertonic lithium or magnesium media. *Bot. Mag. Tokyo* 98: 151–157.

Gross, K. C., Pharr, D. M. and Locy, R. D. (1981) Growth of callus initiated from cucumber hypocotyls on galactose and galactose-containing oligosaccharides. *Plant Sci. Lett.* 20: 333–341.

Göring, H. and Reckin, E. (1968) Einfluss der D-Galactose auf den Kohlenhydratstoffwechsel pflanzenlicher Gewebe. *Flora (Jena)* 159: 82–103.

Hassid, W. Z. (1969) Biosynthesis of oligosaccharides and polysaccharides in plants. *Science* 165: 137–144.

Inouhe, M., Yamamoto, R. and Masuda, Y. (1986) Inhibition of IAA-induced cell elongation in *Avena* coleoptile segments by galactose: its effect on UDP-glucose formation. *Physiol. Plant.* 66: 370–376.

Inouhe, M., Yamamoto, R. and Masuda, Y. (1987a) UDP-Glucose level as a limiting factor for IAA-induced cell elongation in *Avena* coleoptile segments. *Physiol. Plant.* 69: 49–54.

Inouhe, M., Yamamoto, R. and Masuda, Y. (1987b) Effects of indoleacetic acid and galactose on the UTP level and UDP-glucose formation in *Avena* coleoptile and *Vigna* epicotyl segments. *Physiol. Plant.* 69: 579–585.

Jacobs, A. E. M., Oosterhof, A. and Veerkamp, J. H. (1990) 2-Deoxy-D-glucose uptake in cultured human muscle cells. *Biochim. Biophys. Acta* 1051: 230–236.

Jaffe, M. J. and Leopold, A. C. (1984) Callose deposition during gravitropism of *Zea mays* and *Pisum sativum* and its inhibition by 2-deoxy-D-glucose. *Planta* 161: 20–26.

Jaspers, H. T. A. and Van Steveninck, J. (1976) Transport of 2-deoxy-D-galactose in *Saccharomyces fragilis*. *Biochim. Biophys. Acta* 443: 243–253.

Jaspers, H. T. A. and Van Steveninck, J. (1977) Active transport of L-sorbose and 2-deoxy-D-galactose in *Saccharomyces fragilis*. *Biochim. Biophys. Acta* 469: 292–300.

Kratky, Z., Biely, P. and Bauer, S. (1975) Mechanism of 2-deoxy-D-glucose inhibition of cell-wall polysaccharide and glycoprotein biosyntheses in *Saccharomyces cerevisiae*. *Eur. J. Biochem.* 54: 459–467.

Maretzki, A. and Thom, M. (1978) Characteristics of galactose-adapted sugarcane cell line grown in suspension culture. *Plant Physiol.* 61: 544–548.

Ordin, L. and Bonner, J. (1957) Effect of galactose on growth and metabolism of *Avena* coleoptile sections. *Plant Physiol.* 32: 212–215.

Ordin, L. and Hall, M. A. (1968) Cellulose synthesis in higher plants from UDP-glucose. *Plant Physiol.* 43: 473–476.

Sakurai, N., Nevins, D. J. and Masuda, Y. (1977) Auxin and hydrogen ion-induced cell wall loosening and cell extension in *Avena* coleoptile segments. *Plant Cell Physiol.* 18: 371–380.

Sakurai, N., Nishitani, K. and Masuda, Y. (1979) Auxin-induced changes in the molecular weight of hemicellulosic polysaccharides of *Avena* coleoptile cell wall. *Plant Cell Physiol.* 20: 1349–1357.

Standard, S. A., Perret, D. and Bray, C. M. (1983) Nucleotide levels and loss of vigor and viability in germinating wheat embryos. *J. Exp. Bot.* 34: 1047–1054.

Schwarz, R. T. and Schmidt, M. F. G. (1976) Formation of uridine diphosphate 2-deoxy-D-glucose and guanosine diphosphate 2-deoxy-D-glucose in vitro using animal enzymes. *Eur. J. Biochem.* 62: 181–187.

Tanimoto, E., Scott, T. K. and Masuda, Y. (1989) Inhibition of acid-enhanced elongation of *Zea mays* root segments by galactose. *Plant Physiol.* 90: 440–444.

Verma, D. C. and Dougal, D. K. (1979) *myo*-Inositol biosynthesis and galactose utilization by wild carrot (*Daucus carota* L. var. carota) suspension cultures. *Ann. Bot.* 43: 259–269.

Yamamoto, R. and Masuda, Y. (1984) Galactose inhibition of auxin-induced cell elongation in oat coleoptile segments. *Physiol. Plant.* 61: 321–326.

Yamamoto, R., Inouhe, M. and Masuda, Y. (1988) Galactose inhibition of auxin-induced growth of mono- and dicotyledonous plants. *Plant Physiol.* 86: 1223–1227.

Yamamoto, R., Sakurai, N, and Masuda, Y. (1981) Inhibition of auxin-induced cell elongation by galactose. *Physiol. Plant.* 53: 543–547.

(Received September 27, 1990; Accepted February 5, 1991)